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Preliminary Studies on the Biology of Sea Lice, *Caligus elongatus*, *Caligus curtus* and *Lepeophtheirus salmonis* (Copepoda:Caligoida) Parasitic on Cage-Cultured Salmonids in the Lower Bay of Fundy

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PRELIMINARY STUDIES ON THE BIOLOGY OF SEA LICE, *CALIGUS ELONGATUS*, *CALIGUS CURTUS* AND *LEPEOPHTHEIRUS SALMONIS* (COPEPODA:CALIGOIDA) PARASITIC ON CAGE-CULTURED SALMONIDS IN THE LOWER BAY OF FUNDY

by

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ABSTRACT

Hogans, W. E., and D. J. Trudeau. 1989. Preliminary studies on the biology of sea lice, *Caligus elongatus*, *Caligus curtus* and *Lepeophtheirus salmonis* (Copepoda:Caligoida) parasitic on cage-cultured salmonids in the lower Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1715: iv + 14 p.

The biology of three species of sea lice, *Caligus curtus*, *Caligus elongatus* and *Lepeophtheirus salmonis* from Atlantic salmon (*Salmo salar*) cultured in marine waters of the lower Bay of Fundy was examined in 1988-89. Three cage-culture sites in and adjacent to Passamaquoddy Bay were the sites of host examinations for sea lice during a 9-mo period (July through March). Both field and laboratory experiments were completed during the study period. Abundance and distribution of all three species were found to be related to water temperatures in the study area. Increased water temperatures resulted in greater numbers of parasites. *Caligus elongatus* was the most abundant species of sea lice observed, exhibiting prevalence levels of 100% during periods of peak high water temperatures. Intensity of infection of *C. elongatus* during optimal periods was 18 parasites with a range of 5-47 parasites. The life cycle of *C. elongatus* was determined from laboratory culture and field observations to consist of four larval (nauplius, copepodid, chalimus, pre-adult) and one adult phase. The phases were divided into nine stages: Nauplius I and II, Copepodid, Chalimus I-IV, Pre-adult and Adult, separated by molts. Generation time of the parasites was approximately 5 wk at 10-12°C. Observations on the site-finding behavior, food and feeding behavior and pathology of *C. elongatus* are included. *Caligus curtus* was found rarely during the study. It constituted only 0.7% of all specimens of sea lice recovered from cultured salmon. It was found frequently on pollack (*Pollachius virens*) caught in or near the salmon cages; its occasional presence on salmon probably represented a fortuitous infection. Its biology was not examined in detail. *Lepeophtheirus salmonis* was uncommon on cultured salmon during the study period. Prevalence of *L. salmonis* during optimal periods did not exceed 8%, intensity of infection of *L. salmonis* was never more than three parasites per examined fish. Observations on its life cycle, feeding behavior and pathology are included. None of the species observed appeared to cause mortalities of cultured salmon during the study period.

RÉSUMÉ

Hogans, W. E., and D. J. Trudeau. 1989. Preliminary studies on the biology of sea lice, *Caligus elongatus*, *Caligus curtus* and *Lepeophtheirus salmonis* (Copepoda:Caligoida) parasitic on cage-cultured salmonids in the lower Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1715: iv + 14 p.

En 1988-1989, on a procédé à des études biologiques sur trois espèces de pou de poisson: *Caligus curtus*, *Caligus elongatus* et *Lepeophtheirus salmonis*, qui attaquent le saumon de l'Atlantique (*Salmo salar*), cultivé dans le cours inférieur de la baie de Fundy. Trois installations d'élevage en cage marine situées à l'intérieur ou près de la baie de Passamaquoddy, ont fait l'objet d'une étude de neuf mois (de juillet à mars) pour examiner l'incidence du pou de poisson chez cet hôte. Toutes les expériences sur le terrain et les analyses de laboratoire ont été terminées durant cette période. On a conclu que l'abondance et la distribution de ces trois espèces de parasites sont liées aux températures de l'eau de la zone d'étude. La hausse des températures de l'eau ont fait augmenter le nombre de parasites. Nous avons remarqué que le *Caligus elongatus* est le parasite le plus abondant des trois; on lui a attribué un taux de prévalence de 100 pour 100 pendant les périodes de température maximale. Pendant les périodes d'infection optimale, on a compté 18 parasites par poisson, sur une échelle de 5 à 47. Les observations sur le terrain et les cultures en

laboratoire ont permis de conclure que le cycle de vie du *C. elongatus* a quatre phases larvaires (nauplius, copepodid, chalimus et pré-adulte) et une phase adulte. On a divisé les phases en neuf étapes: Nauplius I et II, Copepodid, Chalimus I à IV, étape pré-adulte et étape adulte. Les étapes sont séparées par des périodes de mue. Le temps de génération des parasites est d'environ cinq semaines, à une température de 10 à 12 degrés Celcius. Le présent document contient des observations sur la façon dont le *C. elongatus* cherche son site, sur sa nourriture et ses habitudes alimentaires ainsi que sur ses effets pathologiques. Pendant la durée de l'étude, nous avons trouvé très peu de *Caligus curtus*. Il ne représentait que 0,7 pour 100 de tous les spécimens de poux de poisson prélevés sur le saumon cultivé. Par contre, on l'a souvent repéré chez la goberge (*Pollachium virens*) capturée dans ou près des cages à saumon; sa présence occasionnelle sur le saumon représente probablement une infection fortuite. Nous n'avons pas examiné en détails ses caractéristiques biologiques. Quant au *Lepeophtheirus salmonis*, il s'est rarement manifesté chez le saumon de culture pendant la période visée par l'étude. Aux périodes de pointe, le taux de prévalence du *L. salmonis* n'a pas dépassé 8 pour 100 et nous n'avons jamais trouvé plus de trois parasites par poisson examiné. Notre document présente des observations sur son cycle de vie, ses habitudes alimentaires et ses effets pathologiques. Aucune des espèces observées pendant la période visée n'a semblé provoquer la mort du saumon cultivé.

INTRODUCTION

The culture of Atlantic salmon in the lower Bay of Fundy is a successful and expanding industry. The culture method employed - rearing several thousand fish within cages in close proximity - often predisposes the salmon to epizootics of parasitic and other diseases. In northern Europe and Scandanavia, serious epizootics of sea lice have been responsible for significant mortalities of cultured salmon. It is possible that the salmon culture industry in Norway and Scotland, at least, could not exist without periodic treatments to reduce levels of sea lice. The grow-out methods employed in the lower Bay of Fundy are essentially identical to those used in northern Europe. The lower Bay of Fundy now supports over 40 cage-culture sites, some of which have previously experienced heavy sea lice infections. Little or nothing has been reported on the biology of sea lice in the region.

This paper represents the preliminary findings of a study of the biology of sea lice parasitic on Atlantic salmon (*Salmo salar*) cultured in marine waters of the lower Bay of Fundy funded by the New Brunswick Department of Fisheries and Aquaculture. It describes the results of analysis of data compiled between 1 July 1988 and 31 March 1989, a period of 9 mo. Included are descriptions of the general biology, life histories, pathology and abundance and distributional trends recorded for each species.

MATERIALS AND METHODS

FIELD SAMPLING

Three cage-culture operations within the study area were selected as sampling sites (Fig. 1) to be visited on a regular basis. Several other sites were visited randomly to collect samples of parasites for comparative purposes. The Huntsman Marine Science Centre (site no. 1) possessed one cage of smolt size salmon. A minimum of 20 fish was examined from this cage once a week for the months of July, August, September and October 1989. During November and December 1988, fish were sampled once every 2 wk. From January through March 1989, Huntsman Marine Science Centre salmon were sampled once each month. Cold water temperatures restricted the number of sample periods during winter at all sites. Stress and possible mortality of fish could have resulted from handling while sampling during concurrent cold water and air temperature periods. Site no. 2, the Salmonid Demonstration and Development Farm, in Lime Kiln Bay, was sampled once each month for all months except January and February 1989, when sampling of fish was prohibited. Between 60 and 200 smolt and/or market size salmon were examined at site 2 during each sample period. The third field site studied was the Malloch cage operation in Harbour du Lutre, Campobello Island. At this site (no. 3), smolts were sampled every 2.5 mo, except during January and February, when examinations were prohibited due to cold temperatures. Sampling procedure (see Hogans and Trudeau 1989) at field sites was conducted as follows: fish from preselected cages were localized in one corner of the cage by seine net. Two to six salmon at a time were removed from the cage by small dip net and placed, after examination for sea lice, in a large (225-L) plastic rectangular tank containing a 0.1% anesthetic solution of phenoxyethanol and seawater. The examination of each fish consisted of counting all visible parasites and recording the sites on the host salmon where concentrations of the parasites were observed. After immersion in the anesthesia for approximately 3 min, the fish were removed, measured, weighed and returned to the cages. On three occasions, fish were examined one additional time after removal from the anesthesia. This allowed determination of the proportion of parasites which were removed by the action of the anesthesia. These data were later used to determine levels of infection on salmon which could not be examined initially until after removal from the anesthesia bath. After all fish examined were returned to the cage, the anesthesia solution, containing sea lice dislodged from the salmon, was strained through 0.2-mm mesh sieves. The collected parasites were then transferred to bottles and fixed and stored in 50% isopropyl alcohol. These were returned to the laboratory and the number of each developmental stage, sex ratio of adults and maturation level and

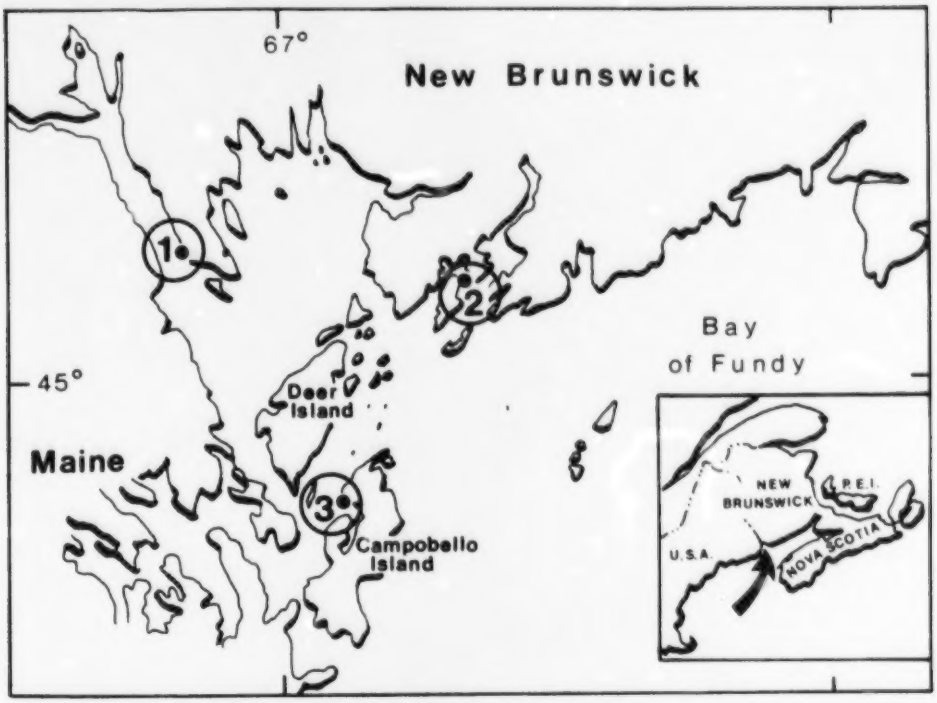

Fig. 1. Map of the study area showing the location of three cage sites sampled during 1988-89.

fecundity of females for each species of sea lice recorded. In addition to the above data, information on environmental parameters, i.e. water temperature, salinity and dissolved oxygen, were recorded, including visual observations of pathology on the salmon caused by infections with sea lice.

LABORATORY ANALYSIS

In addition to field studies, it was necessary to perform experiments within the laboratory to allow frequent monitoring of the life cycle, behavior and pathology of sea lice. The subject of all laboratory methods was one species, *C. elongatus*, due to its overwhelming abundance and relative ease of culture.

Determining the life cycle of *C. elongatus*

To determine the morphology and behavior of the life history stages of *C. elongatus*, salmon smolts were kept in aquaria and infected with *C. elongatus*. Recently molted infective stages were introduced into the aquaria with previously non-infected smolts. Smolts were examined periodically for life history stages; the time between examinations was dictated by our own observations of cultured salmon in the field and by reviews of previous literature on life histories of caligid copepods. The early larval stages were recovered, fixed in 70% ethanol and examined in lactic acid for structural details. The elucidation of the early larval stages allowed detailed sorting of stages collected during field sampling.

To examine the effects of water temperature on abundance of sea lice on salmon, and also to compare laboratory results with those recorded in the field, 20 smolts were kept from August until December 1988, at ambient seawater temperatures. The initially uninfected fish were kept in a 2-m circular tank (supplied by DFO, St. Andrews) with a continuous supply of seawater from an intake near the Biological Station wharf, St. Andrews. Two weeks after introduction, the smolts were subjected to infection with *C. elongatus* adults. Approximately 100 live parasites of both sexes were introduced into the tank after the water supply had been interrupted. After 18 h, the water supply was resumed, the fish examined

(no anesthesia used) and number of sea lice on each recorded. All fish were examined once each month until this experiment was terminated. Detailed records of water temperature were also kept during the experiment.

One other laboratory experiment, utilizing a single smolt in an aquarium, was performed. This single salmon was initially infected with six adult female *C. elongatus*. Observations on the parasites' position on the host, effects of feeding and site of infection preference were recorded every second day from 15 August-31 December 1988 during this experiment. Plankton samples were taken frequently from the water in the aquaria to help in determining production of larval stages. As with other experiments completed in this study, detailed records of water temperature and salinity were also recorded during observation periods.

Three terms appear frequently in this paper in relation to the population dynamics of infection of sea lice studied. The first, prevalence of infection, refers to the percentage of fish infected in a sample. The second, intensity of infection, is the average number of parasites per infected fish. Abundance is a general term encompassing both prevalence and intensity, referring to overall occurrence of the copepods.

RESULTS

THE SPECIES

Three species of sea lice were found on salmon cultured in the lower Bay of Fundy. All three belong to the family Caligidae and hence are of similar external morphology. The species, *Caligus curtus*, *Caligus elongatus* and *Lepeophtheirus salmonis* live on the external body surfaces of the host fish. All are easily visible to the naked eye and two, *L. salmonis* and *C. elongatus*, in particular, have potential as serious pathogens. Each species will be described and its biology discussed in separate sections below.

Caligus elongatus, Nordmann, 1832

Morphology and general biology

This strictly marine species is by far the most numerous of the three species found on salmon in the study area. Unlike *C. curtus* and *L. salmonis* which are parasites of relatively high host specificity, *C. elongatus* has been reported from more than 80 species of marine fishes representing several families, salmonid fishes being particularly often infected (Post 1987). In general appearance, *C. elongatus* (Fig. 2) is golden-brown or yellow in color, averaging about 6-8 mm in total length. The adult females are often observed with two elongate egg strings projecting posteriorly from the body (Fig. 2). Males are smaller than females and possess a longer and slimmer genital segment. All species of *Caligus*, including *C. elongatus*, exhibit disc-shaped lunules near the anterior end of the frontal plate. These, along with other features, serve to distinguish them from *L. salmonis*. The appendages with which the parasite clings to the host skin are located on the ventral surface of the body. The principal appendages of adhesion for *C. elongatus* are the second antennae and maxillipeds (Fig. 3). They are alike in both structure and size between the male and female. *Caligus elongatus* is also equipped with four pairs of swimming legs posterior to the grasping appendages. These enable the parasite to swim about freely, moving along the host body surface and occasionally transferring among hosts.

Life cycle of *Caligus elongatus*

Determined from laboratory culture, *C. elongatus* has a life cycle consisting of four larval and one adult phase. The phases are split into eight larval stages, each separated by a molt during which the larva sheds its old cuticle and replaces it with a new, structurally different one. Females were impregnated by adult males during the pre-adult (last larval stage) or as mature adults. Each female possesses a sperm receptacle which serves to store sperm from the original mating, releasing them gradually as eggs are extruded from the ovaries and subsequently fertilized. Eggs are

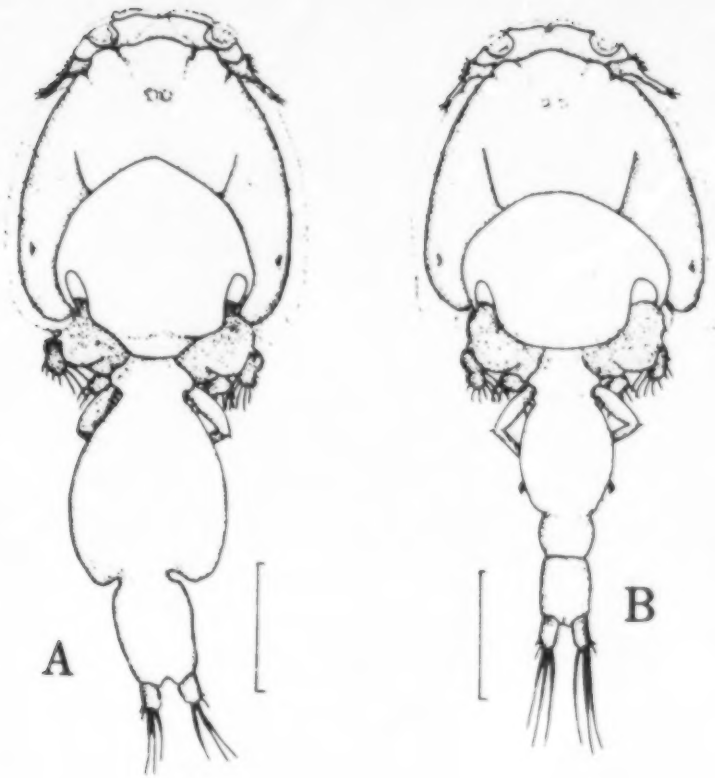

Fig. 2. *Caligus elongatus*, adults. A - female; B - male; dorsal views. Redrawn from Kabata (1979) (scale bar - 1 mm).

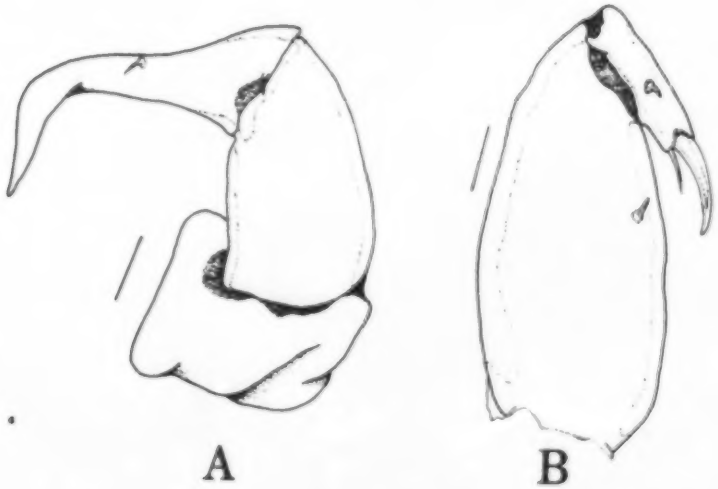

Fig. 3. Grasping appendages of *Caligus elongatus*. A - second antenna, lateral; B - maxilliped, ventral (scale bar - 100 μ).

laid in elongate, cylindrical strings, each egg being disk-shaped. The average number of eggs layed within each string was 89; the number produced was apparently unrelated to environmental parameters such as water temperature. Close observation shows those eggs immediately below and close to the oviduct to contain undifferentiated cell material. Growth and development of the first larval stage can be followed posteriorly along the egg string, the last egg on the end of the string containing fully developed first larval stages ready to hatch. The first larval phase observed was the nauplius. This phase is divided into two stages, Nauplius I and Nauplius II (Fig. 4, 5), by a single molt. These stages are positively phototaxic and utilize their setae-laden appendages to propel them toward light. In the open water of a salmon cage, this is necessarily towards the surface. This behavior is an adaptation of the larval stage to keep it in the vicinity of the salmon which also frequent the surface zone of the cage. Although the naupliar stages are not infective to the host, it is an advantage to remain near areas with numerous hosts until the next larval phase, which is infective, is attained. Occasionally we observed Nauplii II in the mucous layer of some salmon from cage sites. This behavior, i.e. invading host mucous, has not previously been reported. The nauplii are rather feeble swimmers; invasion of the mucous may increase their chances of successfully infecting the host and eliminate the possibility of being swept away from the cage site by tidal movement. Depending upon the water temperature, the first naupliar stage lasts for 15-30 h, low water temperatures (less than 6-8°C) considerably prolonging the length of each stage. The second naupliar stage lasts for approximately the same time period, our study showing a duration of 35 h at 10°C. No molting of any larval stages probably took place below approximately 3°C.

The second nauplius molts into the second phase, the copepodid (Fig. 6). The copepodid is more streamlined, with well developed swimming legs which render it swifter and more mobile than the nauplius. This is an important advantage as the copepodid is the stage which is infective to the host. The copepodid is equipped with a frontal filament used for attachment to the host. During early growth of the copepodid the rudimentary filament lies along the dorsal surface of the body, projecting posteriorly. After the copepodid finds a host, to which it attaches initially using its second antennae and maxillipeds (grasping appendages), the frontal filament migrates forward to project anteriorly from the frontal margin of the body (Fig. 7). The end of the frontal filament becomes attached to a scale on the fish body. There the larva remains tethered through successive molts. The frontal filament is exceptionally strong and flexible. The copepodid is positively phototaxic like the nauplius although this ability appears much more highly developed. The copepodids also possess a degree of chemotaxic sensitivity. Experiments done during this study indicate that when free-swimming within approximately 10 cm of a potential host, the copepodid will invariably swim immediately to the body surface, regardless of light projected from a different direction than that of the host. Beyond 10 cm distance from the host, the copepodid is essentially restricted to phototaxic behavior and will swim towards the strongest light source. The copepodid phase lasted for approximately 50 h at 13°C.

The copepodid molts into the next phase, the chalimus. There are four stages of the chalimus. Chalimus I (Fig. 8) still retains some of the copepodid features such as general upper body shape and small size, but since it is now attached, its swimming legs are not essential and have become reduced. The grasping appendages are similar in size to that possessed by the preceding phase. The frontal filament is somewhat shorter than that exhibited by the copepodid. The genital segment is now obviously differentiated, but still unsegmented. Most of the setae on the first antennae and swimming legs have become shorter and stouter. The first chalimus molts and becomes the second (Fig. 9), which possesses a general morphology more like the adult. The frontal filament has shortened considerably and the carapace (disk-shaped upper body) now shows distinct suture lines and first indications of segmentation. The genital segment is now distinct, and comprises a considerable portion of the parasite. Setae on the appendages and swimming legs are further shortened. The swimming legs are broader, flatter and relatively more massive than those of the

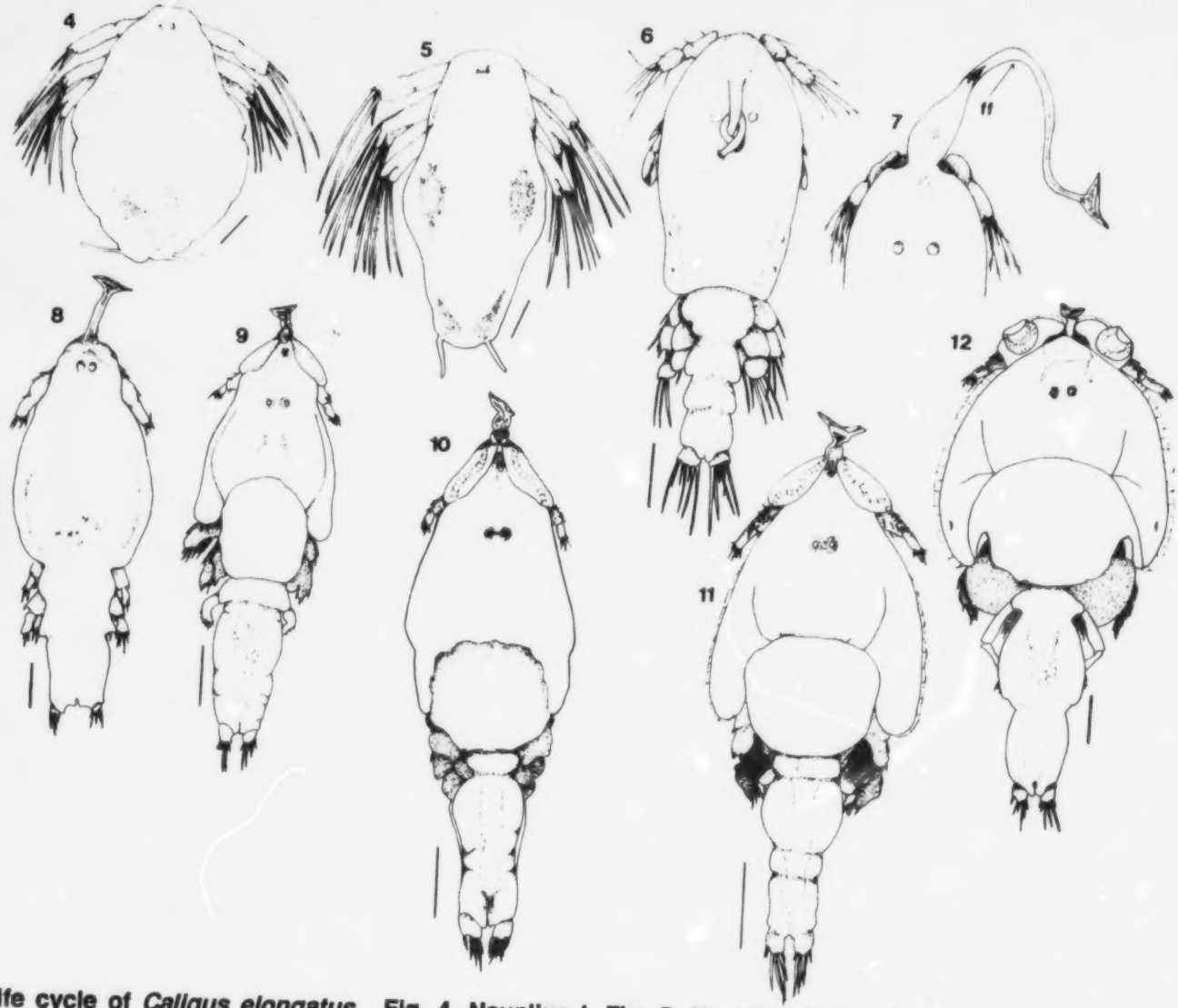

Fig. 4-12. Life cycle of *Caligus elongatus*. Fig. 4, Nauplius I. Fig. 5, Nauplius II. Fig. 6, Copepodid. Fig. 7, Anterior of copepodid with frontal filament extended. Fig. 8, Chalimus I. Fig. 9, Chalimus II. Fig. 10, Chalimus III. Fig. 11, Chalimus IV. Fig. 12, Pre-adult (male). Scale bars - 100 μ: Fig. 4-8; 200 μ: Fig. 9-10; 0.5 mm: Fig. 11-12. All figures in dorsal view (ff - frontal filament).

chalimus I. The frontal plate is also now distinct from the carapace. The next stage, the chalimus III (Fig. 10), resembles chalimus II in most details, but the molt has given rise to new structures and further defined the carapace. The frontal plate now has internal signs of features which will eventually become the lunules. The total length and width of the chalimus III is now noticeably greater than that of the second stage. The fourth chalimus (Fig. 11) is again more long and broad than chalimus III. During the chalimus IV stage, male and female can be occasionally distinguished, males possessing a slimmer and more elongate genital segment. The suturing of the carapace is now essentially adult in character, and the peripheral carapace fringe, also an adult character, is now in place. The appendages and swimming legs are slightly larger than those found on the chalimus III, and will not alter in structure and will become only slightly larger during the next two phases. The frontal filament has not changed in length from chalimus II and III. The swimming legs have reached the end of modification, being now relatively large and armed with pinnate (hair-covered) setae, in preparation for the next phase which detaches from the host body surface.

The last phase before the adult, the pre-adult or juvenile (Fig. 12), is no longer attached by the frontal filament, and is mobile, like an adult. This phase now has fully developed lunules, appendages, carapace, genital segment and swimming legs. The only difference between it and the adult, except for being slightly smaller in size, is the slimness and relative proportions of the genital segment. Males and females are easily distinguished at this stage; males exhibit a first genital segment with rounded posterior corners, females show this segment with truncate, acute corners. The pre-adult molts into the adult. We were not able to determine the time required for each chalimus stage. We postulate that the time required from chalimus I to newly molted adult is about 3 wk at 12°C.

Generation time

The generation time of *Caligus elongatus* determined from laboratory culture was found to be approximately 5 wk at 10°C. The generation time incorporates the period from newly hatched nauplius I to mature adult female. Generation time was directly related to water temperature, low temperatures increasing the time required to complete an entire life cycle, high temperatures decreasing it. Given the water temperature regime of the lower Bay of Fundy, the production of few or no larval stages in water less than approximately 5°C, and that optimum temperatures (approximately 14°C) occur for only short periods during early fall, there are probably only about four to eight generations of *C. elongatus* completed annually in the study area.

Abundance on cultured salmon

Caligus elongatus was the most abundant species of caligid copepod which infected salmon in the study area. Overall the species accounted for 97.3% of all copepods observed and collected during this study. In terms of prevalence, during certain months, *C. elongatus* is found on almost every salmon cultured in the lower Bay of Fundy. Intensities of infection during these months vary.

Seasonality of infection

As *C. elongatus* exhibits short generation times in response to high water temperatures, it is axiomatic that they be most abundant during late summer and the fall when temperatures are highest in this region. The results of the present study support this statement. The prevalence data for *C. elongatus* recorded through time (July through February) for all sites combined (Fig. 13) shows the largest

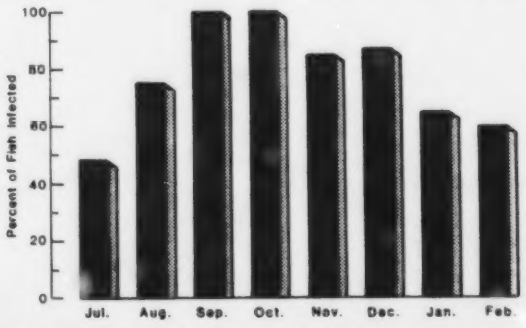

Fig. 13. Prevalence of *Caligus elongatus* on cultured Atlantic salmon from three sample sites (combined) examined in 1988-89.

percentage of fish were infected during the late summer and fall of 1988. These data also show a reduction in the percent of cultured salmon infected during the period from December 1988 through February 1989, when water temperatures fall to yearly low levels. When examined separately, the prevalence data collected at each individual cage site also exemplify this trend. When compared directly with recorded water temperatures, prevalence (Fig. 14) increases with high water temperatures, independent of time or season.

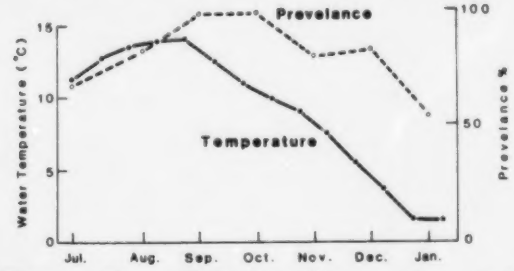

Fig. 14. Relationship of water temperature to prevalence of *Caligus elongatus* on cultured Atlantic salmon from three sample sites (combined) examined in 1988-89.

This has been exemplified by previous laboratory experiments with other caligid copepods. In the lower Bay of Fundy, it is expected to see the greatest number of *C. elongatus* during the months of August through November, given the present climate regime of the region.

Analysis of intensity data from all sites combined (Fig. 15) indicates a trend similar to

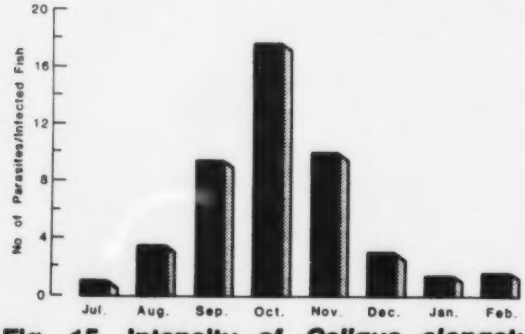

Fig. 15. Intensity of *Caligus elongatus* on cultured Atlantic salmon from three sample sites (combined) examined in 1988-89.

that shown by prevalence. The greatest number of parasites observed on infected fish occur during fall. The fact that the intensity peaks in October, unlike prevalence which is initially (in September) and continuously high through December, is a reflection of the generation time of *C. elongatus*. The greatest number of chalimus stages are present in August and September (Fig. 16). Given the generation time

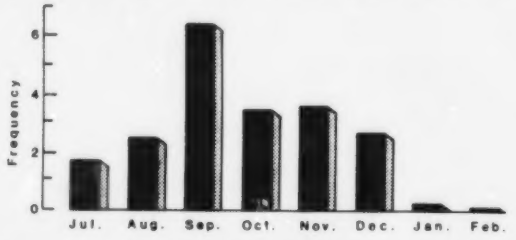

Fig. 16. Frequency of occurrance of chalimus I and II stages in samples collected from cultured Atlantic salmon from three samples sites (combined) during 1988-89.

of the species (about 5 wk at the 10-13°C water temperatures of late summer-early fall) and the predicted age of the oldest chalimus IV larva (3 wk), 2-3 wk additional growth would centre the peak abundance of pre-adults and adults in mid to late October. Levels of intensity were similar between the sites studied. There was a noticeable increase in intensity observed on fish from the study site in Lime Kiln Bay. This site exhibited the highest levels of infection of any site and retained unusually high levels of parasites per fish (over 10 per fish) later in the year (through December) than the other two sites. The reasons for this difference in intensity between sites is unknown. It is probable that environmental conditions are responsible, although the exact parameter is as yet unestablished. The temperature profile for Lime Kiln Bay waters was similar to the other sites, so it is likely that water temperature did not account for this discrepancy. It is possible that the enclosed nature of Lime Kiln Bay and its large concentration of cage sites allow for successful transmission of *C. elongatus*, as compared to the other two sites which are more open and relatively isolated from other sites. Although intensity peaked in October, it fell steadily (in two sites and more gradually at Lime Kiln Bay) through the winter months (through

February), showing a general decline from a high of 17 parasites to a low of 1-3 parasites per fish. Prevalence, however, peaked in September and remained at 80-100% until the end of December. It is apparent that once initially infected, salmon are likely to retain at least a few parasites, regardless of water temperatures, throughout the year. Figure 13 shows a higher level of prevalence in February than July; there is no explanation for this event; it should be the reverse; a lack of samples for February is probably responsible. Based on laboratory observations, cooling water in late fall causes the majority of parasites to leave the host, most of which die soon after. This action accounts for the lower intensity values in winter. Not all parasites leave the host, however, in response to cooler water temperatures, as can be seen (Fig. 15) by the small number of parasites (mostly females) which persist on the host through the winter into spring.

Sea ratio of *Caligus elongatus*

Sex ratios determined during the study pertain only to those phases of the life history during which the sex of the parasite was observable, the pre-adult and adult stages. The numbers of *C. elongatus* of each sex change considerably throughout the year, but females are always in greater supply. The relative percentage of each sex recorded from samples collected from fish at Site No. 1 (HMSC) is shown in Fig. 17. Sex ratios were not analyzed

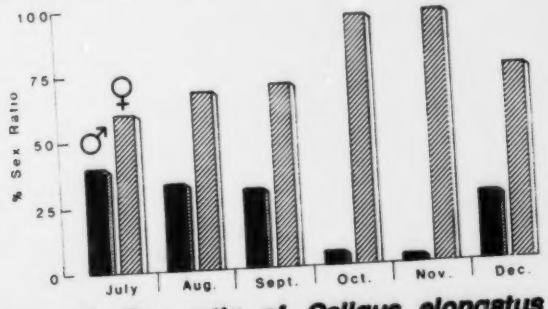

Fig. 17. Sex ratio of *Caligus elongatus* from cultured Atlantic salmon from sample site no. 1 (HMSC) examined in 1988-89.

for the other sites given a lack of time contiguous data for these. Figure 16 shows a greater proportion of females throughout the year, but particularly in late fall and early winter. The reasons for this increased abundance of females are unknown. It is possibly related to one or both of the following factors: 1) more females are produced in late fall so that those *C. elongatus* which remain on the host through the winter are able to begin egg laying immediately on arrival of warmer water temperatures in May and June. This strategy has great advantages for the parasite. Almost all (91.4%) of the females found on fish in December 1988 and January and February 1989 possessed fully extruded egg strings. Although we are relatively sure that the life cycle of *C. elongatus* cannot be completed during the winter, the overwintering females are ready to proceed with egg production and shedding when water temperatures warm up to about 5°C. The eggs extruded in late fall apparently remain dormant and unharmed during the winter months, being eventually released in spring; 2) males are more susceptible to the effects of winter water temperatures than females. They may die more rapidly or be unable to remain on the host as effectively. However, if this were true, it is expected that very few males, if any, would be found. Figure 16 shows that males make up from 10-35% of all *C. elongatus* found in winter, though females greatly predominate. In light of this argument, it appears likely that the reason for female predominance is the first hypothesis.

Site of infection and site-finding behavior of *C. elongatus*

During the free-swimming copepodid phase, *C. elongatus* searches actively for a host. Our preliminary observations suggest that there is no site on the host which is preferred for initial attachment by the copepodid. We found this stage, when attached on most areas of the host body, often widely scattered with no discernable aggregations in any single spot. After anterior migration of the frontal filament on the copepodid and adhesion to a scale, the larvae are unable to change position on the host. Once the pre-adult phase is reached, the parasite breaks its link with the frontal filament. The pre-adults and adults can, like the copepodid, be found on any area of the host body surface. Several parasites do, however, congregate on specific areas of the fish. In

particular, these are the dorsal and lateral surfaces of the head, the anterior portion of the abdomen between the opercula, and near the base of and on the lateral surfaces of the caudal fin. For *C. elongatus*, more adult and pre-adults were observed on the head and anterior abdomen than any other area of the host. From this, we assume that these areas can be considered the preferred site of infection. Given the free-roaming capabilities of *C. elongatus*, these sites must offer the parasites ease of attachment, abundant and easily acquired food and reduce the chance of being physically pushed off the host. In a salmon cage, most all salmon repeatedly come in contact with the flanks of other fish and the netting on the sides of the cage. Being on the dorsal surface of the head or underneath on the abdomen would lessen the chances of being scraped from the fish.

Food and feeding behavior

The effects of feeding by *C. elongatus* on the host are easily seen, even the damage inflicted by a single parasite is obvious. Just after becoming a mobile pre-adult, the parasite moves slowly over the body surface, feeding on the mucous covering of the host. The path left by this "grazing" movement is approximately the width of the carapace and extends from the original point of attachment to one of the preferred sites of infection. Grazing action of the copepod leaves the fishes' skin devoid of mucous along the path, visible as a dark line against the light-colored mucous layer. Once several parasites are in the same area on the host, the mucous covering is soon stripped completely from that area. Once this occurs, the parasites then resort to feeding directly on the skin, musculature and blood of the host. Once in position in a preferred area, the parasites seldom move but remain there throughout the year. The effects of feeding in a single area by several parasites simultaneously causes the occurrence of many circular lesions, each probably representing the initial entry point for the mouth tube of the parasite (c.f. Kabata 1974). In severe cases involving heavy infestations, the parasites continue to feed down through the skin into the subcutaneous musculature, eventually destroying somatic musculature and cartilage. In several cases, this type of damage was often seen on the dorsal surface of the head. When mortalities of salmon result from an infection of sea lice, the final cause of death is usually reported as osmoregulatory failure. The host, stripped of large areas of its protective skin and mucous covering, is unable to maintain essential body fluid levels. It is likely, given the importance of the mucous covering of the fish for its overall health, that large numbers of copepods feeding on the mucous alone would cause mortality. An additional effect of feeding by *C. elongatus* is to allow secondary bacterial infections to begin in areas stripped of mucous, or in epidermal tissue lesions. The bacterial infections alone, or in concert with *C. elongatus*, greatly affect the health of the fish in terms of stress and gross tissue pathology.

Abundance of *C. elongatus* in relation to fish size

During this study, we sampled two size-classes of salmon, market size and smolts. We were able to compare infection levels throughout the year between the two size-classes only at one site (No. 2). There was no significant difference between prevalence on market salmon and on smolts. This was evident for intensity as well. The reason for the similarities in values for fish significantly different in size was probably related to the life history of *C. elongatus*. The restrictions placed by cold winter water temperatures on the life cycle of *C. elongatus* did not allow a significant accumulation of parasites over the course of the year. Therefore, larger fish (market-size salmon), even though in the water in culture longer than the smolts, were not necessarily exposed to greater or more continuous levels of infection with *C. elongatus*.

Caligus curtus

The second species of sea lice found during this study, *Caligus curtus* (Fig. 18), was also the least abundant. It accounted for only 0.7% of all the copepods collected, or approximately 60 specimens. It is so nearly identical to *C. elongatus* that is was probably occasionally counted as such during field examinations. It was so rare in samples collected from fish at the cage sites, however,

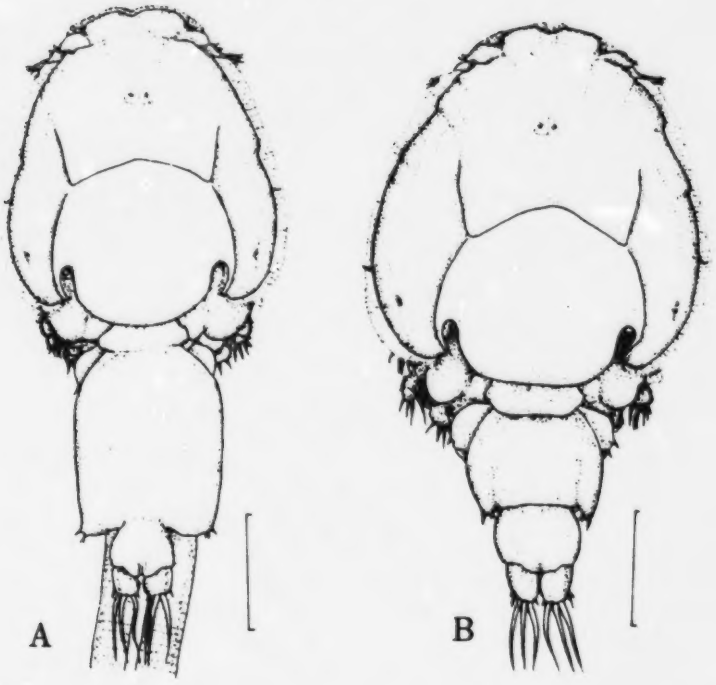

Fig. 18. *Caligus curtus*, adults. A. female; B. male, dorsal views. Redrawn from Kabata (1979) (scale bar - 1 mm).

that rare misidentification in the field was probably insignificant. *Caligus curtus* has not previously been reported from Atlantic salmon. It is usually found on gadoid fishes such as cod, haddock and pollack. Given the abundance of pollack around most salmon cage sites, there is every possibility that some transmission takes place. The rarity of *C. curtus* on the salmon in the presence of so many hosts (pollack) indicates that these are accidental infections of salmon and probably of little concern from a pathogenic point of view.

Given the nature of the infection of *C. curtus* on salmon, it is not relevant to discuss its biology in detail. A few observations on its biology are helpful for comparative purposes. *Caligus curtus* differs from *C. elongatus* largely in the relatively greater width of its carapace and genital segment and in appendage structure. It is larger than *C. elongatus*, about 7-10 mm in length for adult females. In coloration, it resembles *C. elongatus*, being usually gold or yellow - the males, however, are often ivory or pale white. There is no information (previous, or collected during the present study) on its life history, population biology or pathology.

Lepeophtheirus salmonis

Lepeophtheirus salmonis (Fig. 19) is the third and largest species of copepod found on salmon in the study area. Although a major pathogen of, and found in great abundance on, cultured salmon in northern European waters, *L. salmonis* was not numerous in the lower Bay of Fundy in 1988-89. *L. salmonis* represents, in the traditional sense, the term sea lice, as this species is found on wild salmon which are caught in estuaries and the mouths of rivers during spawning migrations. Unlike *C. elongatus*, *L. salmonis* is a parasite of relatively high host specificity, being found only on one family of fishes, the Salmonidae. They are large copepods, 7-18 mm in length for adult

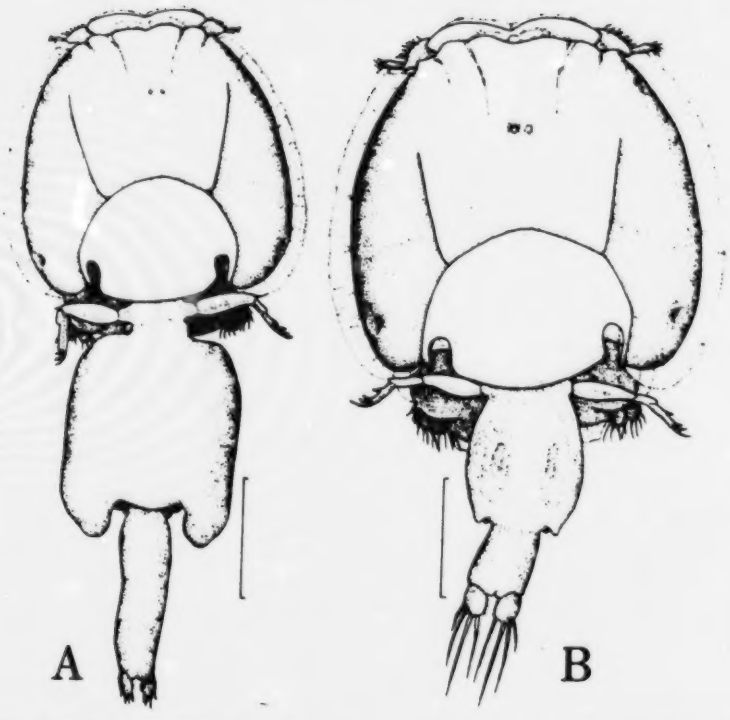

Fig. 19. *Lepeophtheirus salmonis*, adults. A. female; B. male, dorsal views. Redrawn from Kabata (1979) (scale bar - 1 mm).

females, easily observable on the host. In coloration, the body ranges from light brown to olive or pale green, older specimens tending to be olive colored. The carapace is much more round in *L. salmonis* than in *Caligus* and the genital segments much broader. *Lepeophtheirus* has no lunules. Its grasping appendages are similar to those of *Caligus*, but relatively more massive. Males of *L. salmonis* are smaller than females with a broader carapace and short, slim genital segment. *L. salmonis* also possesses well developed swimming legs which it uses to propel itself over the host body surface and to transfer among hosts.

Life cycle of *L. salmonis*

The life cycle of *L. salmonis* has never been adequately described, except for the nauplii and copepodid stages. No detailed descriptions of later larval stages have been published. It is extremely difficult to differentiate early life history of any species of caligid copepod; *L. salmonis* is no exception. Its nauplii and copepodids are almost identical to, though slightly larger than, *C. elongatus*. During this study we have collected adults, pre-adults and chalimus III and IV stages. As most caligid copepods have similar life histories, it is probable that *L. salmonis* possesses nauplii, copepodid, chalimus, pre-adult and adult phases, separated by nine stages, essentially like that exhibited by *C. elongatus*. The females possess long egg strings which are visible against the host body surface. Each egg string contains an average of 96 eggs of the same shape as those of *Caligus*. Generation time (from recently hatched nauplius to mature adult) is proposed, based on previous literature, as approximately 6 wk at 9°C. As with *C. elongatus*, *L. salmonis* generation time and abundance is directly related to ambient water temperature. High water temperatures decrease generation time and increase overall abundance.

Abundance on cultured salmon

L. salmonis accounted for only 2% of the copepods observed and collected from cultured salmon during field sampling. Its level of prevalence during most months was rarely more than 1% and never more than 8% (relative to sample size); the largest number of fish were infected in mid fall (October), soon after periods of annual peak high water temperatures (Fig. 20). Intensity of infection follows a similar trend with highest values also

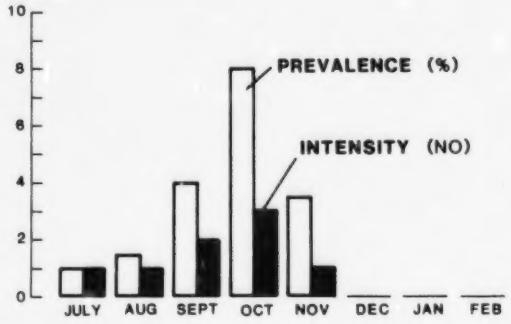

Fig. 20. Prevalence and intensity of *Lepeophtheirus salmonis* on cultured Atlantic salmon from three sites (combined) examined during 1988-89.

recorded in fall. Intensity is never high at any time during the year when compared to *C. elongatus*. Apparently *L. salmonis* disappears from cultured salmon completely during winter months and low water temperatures. The low values for prevalence and intensity for *L. salmonis* recorded during this study were probably related to two factors. These are: 1) since the parasite is unable to overwinter on the host, it is likely that all new infections acquired by cultured salmon in spring are the results of chance transmissions from wild salmon passing by the cage sites during their spring migrations to spawn in the rivers in the vicinity of the culture sites. There is a possibility that *L. salmonis* does not die in winter but remains dormant on bottom until optimal water temperatures are reached in spring. This adaptation is still not sufficient to ensure high levels of prevalence and intensity during optimal periods due to the likely high attrition of dormant parasites in winter (e.g. dormant parasites removed from the vicinity of the cage sites by tidal movements, predation, etc.); 2) *L. salmonis* may have to compete for space and available food with *C. elongatus*.

Food and feeding behavior

Although we did not undertake any laboratory experiments using specimens of *L. salmonis*, some information can be gathered from previous studies on its food habits. *L. salmonis* is proposed as feeding almost exclusively on the blood of the host (Brandal and Edgidius 1976). Observations during the present study show very little disturbance of the mucous layer of salmon infected only with *L. salmonis*. In contrast to signs of mucous grazing, fish infected with *L. salmonis* often show only small swellings of haemorrhagic origin. These appear similar to those caused by several *C. elongatus* specimens concentrated in an area from which the mucous has been completely stripped. European cultured salmon heavily infected by *L. salmonis* often show cranial musculature damage similar to that described herein as caused by *C. elongatus*. It is probable that given its large size and food preference, *L. salmonis* would be very destructive when abundant in the study area.

FUTURE CONSIDERATIONS REGARDING SEA LICE ABUNDANCE

The aquaculture of salmon in northern Europe and Scandinavia is presently a successful and profitable industry. However, nearly every salmon grow-out site in both Norway and Scotland must chemically treat sea lice infections at some point during the year (usually in early fall) to avoid massive mortalities of fish. Large numbers of cage operations provide a basis for sea lice populations, keeping an abundant supply of the parasites for transmission at optimal periods during the year. In Europe, winter water temperatures do not drop as low, or remain as cold, as is characteristic of water temperatures in the Bay of Fundy. This is probably the reason why *L. salmonis* dominates on European cultured salmon; being able to overwinter on the host has advantages in terms of successful spring-summer population growth. There is a distinct possibility that the infection levels of sea lice may increase through time (over

several years) here in the lower Bay of Fundy as they did in Europe. One species, *C. elongatus*, has successfully exploited the resources of Atlantic salmon provided by the local aquaculture industry. It is likely that annual chemical treatments of infected salmon may be required in our region in the foreseeable future.

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